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Fragmentation of Neanderthals' pre-extinction distribution by climate change

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ABSTRACT

Neanderthals lived in Eurasia alongside anatomically modern humans (AMHs) until some 40,000 years ago. The extinction of Neanderthals is attributed to either climatic change, or to the effect of competition with AMHs. We used fossil occurrence records and paleoclimatic data to model the potential distributions of *H. sapiens* and *H. neanderthalensis* using Species Distribution Models, and calculated the degree of habitat quality and connectivity at successive time steps. We found that both species potential geographic ranges progressively retreated from their northeastern borders beginning with 44 ka. Although the degree of habitat loss is similar for the two species, the potential range for *H. sapiens* was constantly some 50% larger on average. The degree of habitat fragmentation, and the size, number, and average distance between optimal habitat patches was initially very similar for the two species. However, all these landscape metrics showed a progressive deterioration for *H. neanderthalensis* only over time. At the end of their existence, the most suitable habitat patches for Neanderthals were small and isolated, and their inferred climatic niche width was statistically narrower than in *H. sapiens*. This does not mean that climate worsening drove Neanderthals extinct, yet it suggests extinction risk for the latter markedly increased over time, towards its actual extinction date.

1. Introduction

It is often thought that Neanderthals were the hominin species best adapted to live under the cold conditions of the Pleistocene. Many features in their bodies are recognized as adaptations to such harsh climates (Steegmann et al., 2002). The large nasal cavity was useful in humidifying and warming cold and dry air during inhalation (Churchill, 1998). As compared to Anatomically Modern Humans (AMHs), Neanderthals were shorter and stouter, had wider chest, and shorter limbs, all of which helps heat preservation (Helmuth, 1998; Holliday, 1997). Despite this apparent propensity to live under rigid climates, Neanderthals did not survive into the coldest phase of the last glacial period. Their extinction is statistically placed around 40 ka (Higham et al., 2014), during marine isotopic stage 3 (MIS 3), and almost in coincidence with Heinrich Event 4, which is a sudden, global shift towards colder temperatures (HE4, Van Meerbeeck et al., 2009). Bradtmöller et al. (2012) proposed the Repeated Replacement Model (RRM) to explain population and cultural breakdown among Neanderthals during Heinrich Events 5 and 4 (at ca. 45 and 40 ka, respectively, López-García et al., 2013; Müller et al., 2011). Under RRM, climatic deterioration is the main driver of *H. neanderthalensis* extinction. In fact, many authors agree that colder climates drove Neanderthals extinct (Finlayson and Giles-Pacheco, 2000; Sepulchre et al., 2007; Stewart, 2004, 2007). However, the last Neanderthals also had to compete with AMH populations. Negative interactions between the two species are often viewed as the potential driver of *H. neanderthalensis* extinction, in alternative to climate change. Hortolà and Martínez-Navarro (2013) even took the extreme view of considering the extermination of Neanderthals as a non-special branch of megafauna extinction, propelled by habitual killing of Neanderthal individuals by AMHs. However, the intensity of competition between Neanderthals and AMHs might have been low. Stable isotope analysis on the enamel of AMHs contemporary to the last Neanderthals revealed a wider niche breadth for the former. AMHs diet included vertebrate meat, fish and/or shellfish and a sizeable amount of

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plant food (Ben-Dor et al., 2016; Hockett and Haws, 2005). In contrast, some authors argued Neanderthals had a less diverse diet centered on large and medium-sized terrestrial herbivore meat (Salazar-García et al., 2013). However, the difference in nutritional ecology between the two species is not entirely clear, and it is in fact possible that Neanderthals exploited a resource spectrum nearly as wide as AMHs (Bocherens et al., 2014; Fiorenza et al., 2015; Henry et al., 2014; Smith, 2015). Gilpin et al. (2016) investigated the interactions between AMHs and Neanderthals taking into account cultural development. According to their results, the faster learning skills of AMHs may have promoted competitive exclusion of a larger population, the Neanderthals, by an initially rare competitor. This model has the merit to show that competition alone could have, in principle, driven Neanderthals extinct.

At some point, Neanderthals and ancient *H. sapiens* populations even interbred. Green et al. (2010) found that between 1 and 4% of the genome in Eurasians is inherited from Neanderthals, despite purifying selection in *H. sapiens* might have removed a number of alleles from the introgression between the two species (Castellano et al., 2014; Sánchez-Quinto and Lalueza-Fox, 2015). The strong evidence for interbreeding between Neanderthals and AMHs poses a question about the real nature of the interaction between the two species, and further complicates our understanding of the role of AMHs in *H. neanderthalensis* extinction. As such, several studies now support the view that *H. neanderthalensis* extinction was likely due to a combination of factors, rather than the product of a single, dominant cause (Rey-Rodríguez et al., 2016).

Competition and climatic tolerance together define a good portion of a species ecological niche (Dormann et al., 2010). To understand whether climate change had any effect on Neanderthals extinction it is fundamental to define the climatic niche first. Furthermore, evidence for competition with AMHs rests on a basic yet untested hypothesis, which is if the niches of the two species were overlapping. Besides trying to decipher the amount of niche overlap between AMHs and Neanderthals, and individual niches characteristics from controversial data (such as palaeodietary reconstructions, aging and positioning of fossil sites and their cultural content) we propose the two climatic niches should be statistically defined, and compared, first. This is further welcome because the cultural identification of Middle Palaeolithic toolmakers can be troublesome (Bar-Yosef and Bordes, 2010; Benazzi et al., 2011, but see Zilhão et al., 2015) dating of such layers can be uncertain (Higham et al., 2014), and climatic (Benito et al., 2017) and dietary preferences of Neanderthals are not entirely clear (Ben-Dor et al., 2016; Bocherens et al., 2014; Fiorenza et al., 2015; Hardy and Moncel, 2011; Henry et al., 2014).

In this paper, we use Species Distribution Modelling (SDM) to quantify and compare statistically the inferred climatic niches of *H. sapiens* and *H. neanderthalensis* in Western Eurasia during the last 8 ka of Neanderthals existence. Eurasian Neanderthals during the 48 to 40 ka interval formed a genetically uniform and distinctive population, which invaded Western Europe from the East after a local extinction (Dalen et al., 2012; Fabre et al., 2009). We studied climatic niche evolution and overlap in the two *Homo* species, identified their optimal habitat patches and to which degree these patches connected to each other.

2. Materials and methods

2.1. Occurrence records

We collected *H. neanderthalensis* occurrence data from three datasets, the Radiocarbon Palaeolithic Europe Database (Vermeersch, 2015), the Stage Three Project archaeological database (van Andel, 2002), and the Canadian Archaeological Radiocarbon Database (CARD, Gajewski et al., 2011). *Homo sapiens* occurrence data were collected mainly from CARD. We decided to keep as valid only occurrences that can be confidently linked to either *H. neanderthalensis* or *H. sapiens*, discarding sites/layers with uncertain taxonomic attribution, or dating. We decided to consider radiocarbon records computed by using Accelerator Mass Spectrometry (AMS) only. Dates were calibrated under the 'intcal13' curve, by using the R package 'Bchron' (Parnell, 2016). The full dataset with details about the dating is accessible as supplementary information (Data Set S1, Fig. S1). For the two species, we extracted occurrence records covering the 60–36 ka period (uncalibrated radiocarbon ages) in order to capture the highest amount of information on the climatic niches of the two *Homo* species during this time interval, while maintaining a sizeable number of occurrence records. The choice of these temporal limits is not casual, since it has been demonstrated that European Neanderthals after 48 ka did form a homogeneous population with little mitochondrial genetic variation (Dalen et al., 2012) and HE5 climatic turmoil paved the way for AMHs invasion of Europe (Müller et al., 2011). Indeed, AMHs were extremely rare in Western Eurasia prior to 40 ka (Benazzi et al., 2011). Yet, it is important to notice that the palaeoecological techniques we applied here (see below for the full explanation) are suited to project species niches in space and time, which makes it feasible comparing species potential niches even outside their temporal occurrence limits.

Once the species records were extracted, we removed duplicated records falling in the same cell of the climatic grid used for the model calibration (see below). After this procedure, we obtained the following numbers of species occurrences: 135 records for *H. neanderthalensis* and 104 records for *H. sapiens* (Fig. S1).

2.2. Climatic predictors

Simulations of past climates for the considered time frames were derived from the global ocean–atmosphere climate model of Singarayer and Valdes (2010). The model is provided with a temporal resolution of 4 kyr and a spatial resolution of $3.75^{\circ} \times 2.5^{\circ}$ based on the Hadley Centre climate model (HadCM3). Downscaled climate simulations from this ocean–atmosphere climate model were taken from Maiorano et al. (2013) at 0.5° of spatial resolution. Specifically, the following four climatic predictors were derived: i) mean temperature during summer, ii) mean temperature during winter, iii) mean precipitation during summer and iv) mean precipitation during winter. Winter and summer temperatures and precipitations define most of the climatic variability relevant to *Homo* (Davies and Gollop, 2003). We preferred using intra-annual ranges rather than annual means to maintain a fair representation of yearly climatic variation. Predictors were re-projected adopting a Mollweide equal area coordinate reference system at a final spatial resolution of ca. 50 km. Absence of multicollinearity among the four predictors was checked, reporting a variance inflation factor < 5 (Zuur et al., 2010).

2.3. Species distribution models

To model species distributions we pooled occurrence and climatic data together across all the time intervals where the two species occur (see Maiorano et al., 2013; Nogués-Bravo, 2009). This approach reduces the effect of environmental truncation (Guisan et al., 2014) on niche estimation by including the highest possible amount of information on niche characteristics. It also smoothens the problem of dating uncertainty of individual fossil sites. However, to tackle more effectively the problem of dating accuracy, we produced around each calibrated AMS date estimate a uniform distribution of dates ranging over the 95% confidence interval around the date. Then, we randomly sampled a single date within this range, and performed SDM evaluation. This procedure was repeated 100 times, and SDMs results of the 100 replicated were eventually averaged. For each species and SDM replicate, we randomly generated a set of 10,000 background points over Eurasia, which were used as pseudo-absences together with observed presences to calibrate the SDMs. The 10,000 pseudo-absences were subdivided across the time periods where each species occurred, proportionally to the size of the occurrence records falling into each interval. SDMs were calibrated using an ensemble forecasting approach,

as implemented in the biomod2 package (Thuiller et al., 2009) within the R environment. We considered the following four modelling algorithms: Generalized Linear Models (GLMs); Generalized Additive Models (GAMs), Generalized Boosted Regression Models (GBMs) and Maximum Entropy (MAXENT). Each species occurrence dataset was randomly split into a 70% sample, used for the calibration of the model, and the remaining 30%, used to evaluate the model performance. Models' predictive performance was assessed measuring the area under the receiver operating characteristic curve (AUC), and Boyce index (Hirzel et al., 2006). The splitting procedure for model evaluation was repeated 10 times and evaluation scores and projections were averaged. To avoid using poorly calibrated models, only the projections from the models with AUC > 0.7 were considered in the subsequent analyses. Models were averaged calculating a weighted mean by model's AUC (Marmion et al., 2009). SDMs were projected over Eurasia on three specific moments, i.e. at 48 ka, at 44 ka, and at 40 ka, in keeping with the temporal resolution of the climatic data. The three models projections were transformed into binary maps of species presence and absence, using the threshold that maximizes the sum of sensitivity and specificity (Di Febbraro et al., 2015; Maiorano et al., 2013). To assess the effect of model extrapolation on values of predictor variables lying outside the training range, i.e. projecting models on non-analogous climates (Nogués-Bravo, 2009), we conducted a MESS analysis (see Fig. S2), following Elith et al. (2011).

2.4. Evaluation of structural connectivity

To evaluate the degree of structural connectivity between optimal habitat patches as predicted by SDMs for the two species separately and at each time projection, we calculated the following landscape metrics, as implemented in the Fragstats software (McGarigal et al., 2012): Number of Patches (NP), Area_weighted mean patch area (AREA_AM), Area_weighted mean patch Euclidean distance (ENN_AM), Clumpiness Index (CLUMPY); Proportion of Like Adjacencies (PLADJ); Patch Cohesion Index (COHESION); Effective Mesh Size (MESH); Splitting Index (SPLIT) and Aggregation Index (AI). Optimal habitat patches for each species at 48, 44, and 40 ka time points were identified by progressively binarizing continuous SDMs predictions (i.e. averaged from the 100 replicates) according to a threshold ranging from the 50th to the 95th percentile of the suitability values predicted by the ensemble forecasting, with a step of 1. The landscape metrics were then calculated for each of the 46 (50th to 95th percentile) resulting binary maps. Such metrics are highly dependent on the amount of suitable habitat for a species in a landscape and tend to be strongly correlated to each other (Wang et al., 2014). Therefore, it is often difficult to disentangle the distinct components of landscape structure (e.g., the amount and configuration of habitat) when analyzing landscape patterns (Wang et al., 2014). As we were mainly interested in testing differences in spatial configuration between optimal habitat patches of the two *Homo* species, we sub-selected those landscape metrics exhibiting a low mutual correlation, i.e. Pearson $|r| < 0.7$, with the area of the predicted distribution for each species and time interval. Subsequently, we excluded highly correlated landscape metrics by considering the same correlation threshold. The remaining metrics, that is NP, ENN_AM and COHESION, along with their interaction terms with time intervals, were included into a GLM with a binomial response (*H. neanderthalensis* ["0"] vs *H. sapiens* ["1"]), in order to test for statistically significant differences in these metrics among the optimal habitat patches of the two species. A stepwise model selection based on the Akaike Information Criterion (AIC) was implemented. To assess GLM goodness-of-fit we computed Nagelkerke's adjusted R^2.

2.5. Ecological Niche Factor Analysis (ENFA) and niche overlap

To better evaluate niche characteristics of the two *Homo* species and their evolution through the time steps, we used Ecological Niche Factor Analysis (ENFA, Hirzel et al., 2002). ENFA is a well established approach to derive species climatic preferences from point data (Hirzel et al., 2002), and can be used to rank species according to their different susceptibility to climate change. ENFA analyzes the position of the niche in the ecological space by comparing the distribution of ecological predictors values between species occurrences and the global area. Such niche position is evaluated in terms of *marginality* i.e. the squared distance of the niche barycenter from the mean available habitat, *specialization* i.e. the ratio of the ecological variance in mean habitat to that observed for the target species and *tolerance* i.e. the reciprocal of specialization (Hirzel et al., 2002). A high marginality indicates that a species occurs in very particular environments as compared to the background environmental variation. High specialization corresponds to a narrow niche relative to the habitat conditions available to the species (Hirzel et al., 2002). High tolerance indicates that a species tolerates large variations from its optimum conditions (Simard et al., 2009) and therefore shows broad niche (Braunisch et al., 2008). We focused on marginality and tolerance, calculating these metrics for the two *Homo* species at each time point and for each of the 100 dating replicated datasets (see above). For each species, time point and replicated dataset, statistical significance of marginality and tolerance was evaluated by means of Monte-Carlo randomization (for details see Calenge, 2006). All the procedure was performed using the R package *adehabitatHS* (Calenge, 2006). Statistical differences in niche marginality and specialization through time points between *H. neanderthalensis* and *H. sapiens* were evaluated using ANOVA and post hoc Tukey Honest Significant Differences test (Tukey HSD).

After ENFA, we compared the degree of overlap between the two species. To this aim, we calculated the niches in a gridded and smoothed Principal Component Analysis (PCA) environmental space, taking into account climatic variables over the study area for each time frame, as in Broennimann et al. (2012). We represented the available climatic space of the two species (i.e. all the climatic conditions occurring in Eurasia during the selected time period) by pooling climatic data together for the 60–36 ka time intervals (climatic data occur in 4 ka long frames) and by using these to calibrate a PCA. Subsequently, we projected the values of climate variables corresponding to species locations in the 48 ka, 44 ka and 40 ka time steps into the PCA space to delineate the partial niches of the two *Homo* species in these three different moments. The degree of niche overlap was eventually estimated by means of Schoener's D (Schoener, 1970; Di Febbraro et al., 2017) ranging from 0 (no overlap) to 1 (complete overlap).

3. Results

3.1. SDMs predictions of Homo habitat preferences

SDMs reached excellent predictive performances (Table S1). We found both *Homo* species distributions as primarily driven by temperature during the coldest and the warmest seasons (Fig. 1). Response curves of both species are highly overlapping, suggesting close similarity between Neanderthals' and AMH's potential climatic preferences. However, *H. sapiens* curves tails partly exceeded those of *H. neanderthalensis* for three of four predictors, namely temperature during summer and both precipitation variables, suggesting a wider tolerance to these predictors by *H. sapiens* (Fig. 1).

3.2. Range size and structural connectivity

Predicted distributions of both *H. neanderthalensis* and *H. sapiens* showed a slight though constant reduction over time, especially along their northern-eastern boundaries of their geographic ranges (Fig. S3). *H. neanderthalensis* reduced its predicted distributions of 6.5% from 48 ka to 44 ka, and a further 9.4% from 44 ka to 40 ka. Overall, the territory loss is of some 16% over 8 kyr, equivalent to ca. 600,000 km^2. The corresponding figures for *H. sapiens* are 4.8% reduction from 48 ka to 44 ka, and a further 13.0% from 44 ka to 40 ka, which amounts to nearly 1.2 million km^2 (Figs. 2, S2).

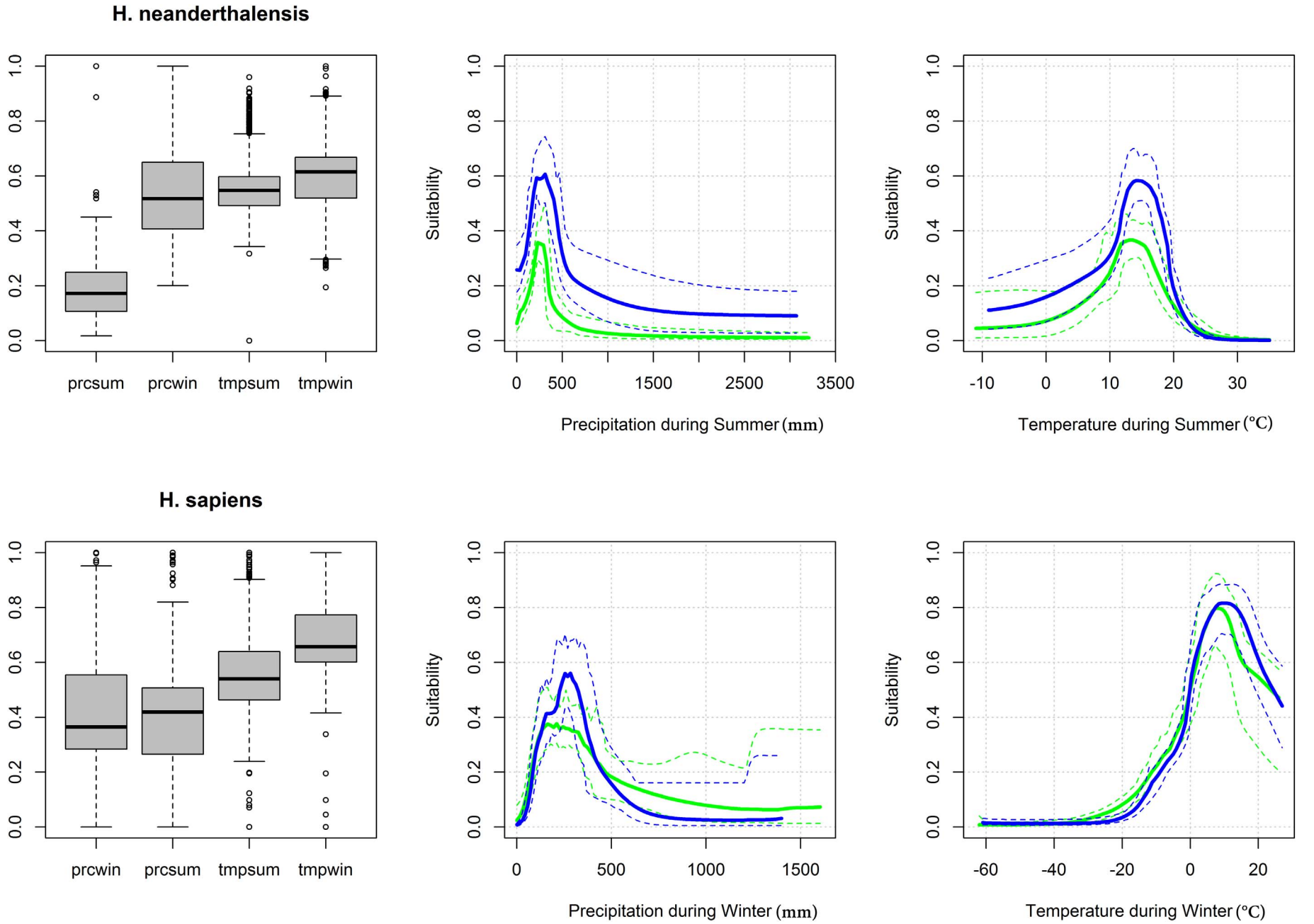

Fig. 1. Relative contribution to the models and related response curves of each climate predictor. Variables in the box plots are listed in order of importance from left (low importance) to right (high importance). Response curves depict the variation of the probability of presence versus each variable, with blue (green) curves referring to *H. neanderthalensis* (*H. sapiens*). Dotted lines represent the range interval over the 100 SDMs run per species in order to account for dating uncertainty. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

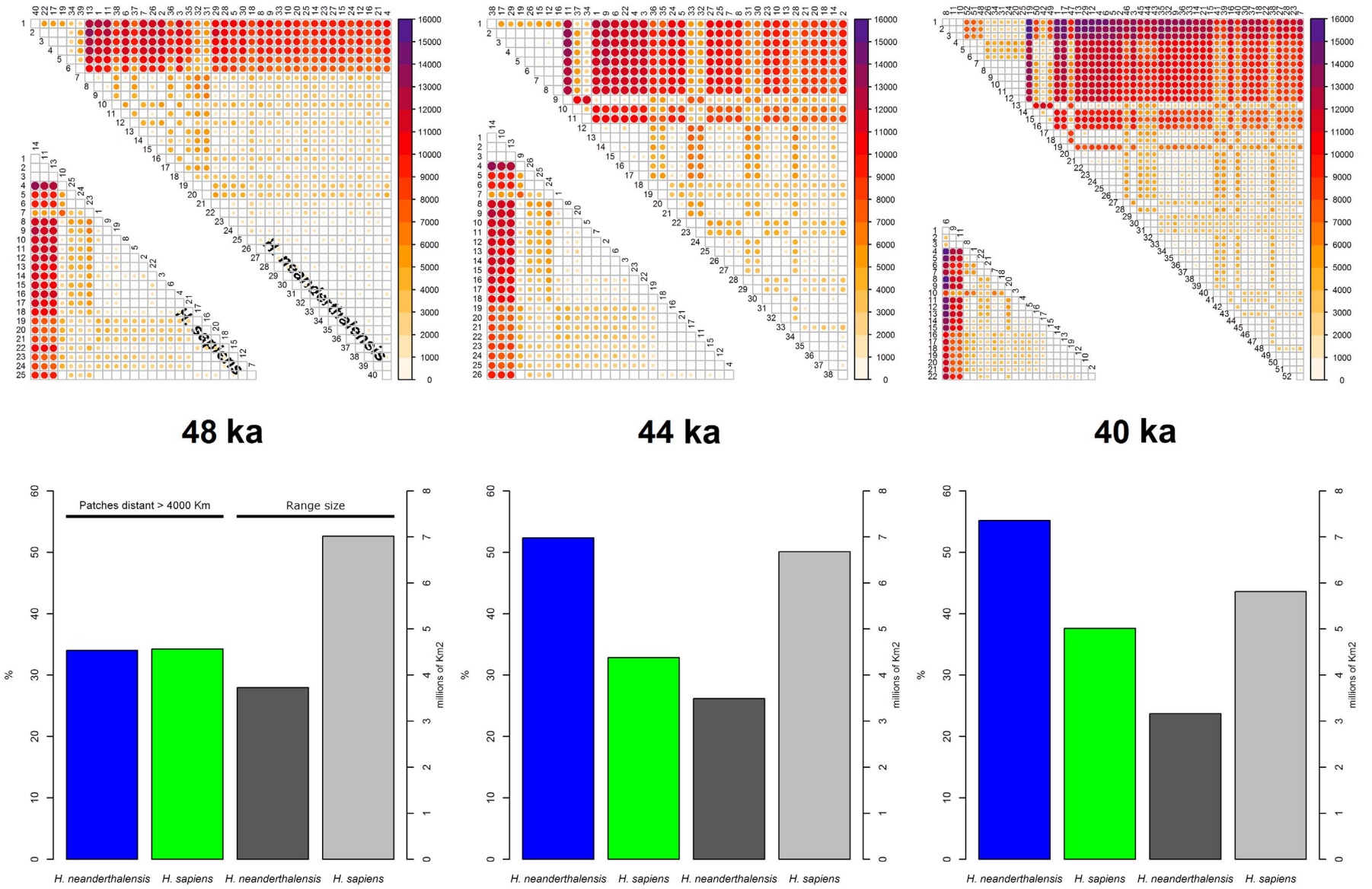

Fig. 2. Evolution of optimal habitats in Neanderthals and AMHs. Dots depict the linear distance in kilometers between optimal patches pairs (i.e. above the 95th percentile of the suitability values predicted by the ensemble forecasting). Distance increases from white to purple and is proportional to dots size. Row and column numbers refer to the individual patch ID. Blue (green) columns in bar plots summarize the percentage of optimal patches pairs > 4000 km apart for *H. neanderthalensis* (*H. sapiens*) in the three time points. Dark grey (light grey) bars indicate range size of *H. neanderthalensis* (*H. sapiens*) in millions square kilometers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Landscape metrics. Selected landscape metrics slope (Estimate) and standard error (St. error) estimates and the p value for the test for differences between the two species (p). The acronym referring to individual metrics is explained in the text.

Coefficients	Estimate	St. error	p
Intercept	0.04631	0.16708	> 0.05
NP	−1.45212	0.25415	< 0.001
ENN_AM	0.18538	0.33813	> 0.05
COHESION	1.45023	0.30625	< 0.001
ENN_AM:44 ka	1.17464	0.65828	> 0.05
ENN_AM:48 ka	0.97142	0.60475	> 0.05
COHESION:44 ka	1.50920	0.64470	< 0.05
COHESION:48 ka	1.34968	0.61127	< 0.05

Although the absolute range size reduction is greater in *H. sapiens*, its potential geographic range was constantly 1.8–1.9 times larger than the Neanderthal's range.

As for structural connectivity analysis, stepwise AIC model selection drops only the interaction term between NP and time intervals, while retaining all of the remaining terms in the final model. The resulting GLM outcomes indicate statistically significant differences in the spatial configuration of the two *Homo* species predicted distributions, reporting a Nagelkerke $R^2 = 0.59$. A statistically significant association emerged between the distributions of *H. neanderthalensis* and lower COHESION values (Table 1; Fig. 2).

In addition, we found a significantly higher number of patches in *H. neanderthalensis* predicted distributions compared to *H. sapiens*, irrespectively of the time steps (Table 1; Fig. 2). Finally, there was no significant difference in mean patch distance between the two *Homo* species distributions (Table 1; Fig. 2). Despite its smaller absolute range, the number of isolated patches within the Neanderthal range is statistically higher than with *H. sapiens*, and these patches are less connected to each other. Importantly, focusing on optimal patches (i.e. above 95th percentile of the suitability values) a clear temporal trend in the data emerges. Optimal patches predicted at 48 ka show negligible differences in their spatial configuration between the two species, but as time progressed structural connectivity within *H. sapiens* range remained almost constant, whereas that of Neanderthals steadily deteriorated. The number of optimal patches > 4000 km apart in Neanderthals rose from 34% for the SDM projection at 48 ka, to > 55% at 40 ka. The corresponding figure for *H. sapiens* changed from a mere 34.2% to 37% (Fig. 2).

3.3. Evolution of niche characteristics

Monte-Carlo randomization tests reported significant marginality and tolerance values for each species, time point and replicated dataset. More importantly, ANOVA indicated significant differences in both niche marginality ($F = 5$, $df = 151.3$, $p < 0.001$) and tolerance ($F = 5$, $df = 579.9$, $p < 0.001$) between the two *Homo* species and the three time moments. Specifically, the related post hoc Tukey HSD reported significantly higher niche marginality by *H. neanderthalensis* irrespectively of the time point (values are reported as standardized difference in means between *H. sapiens* and *H. neanderthalensis*; 48 ka: difference = −1.32, $p < 0.001$; 44 ka: difference = −1.80, $p < 0.001$; 40 ka: difference = −1.14, $p < 0.001$; Figs. 3, S4, S5). On the other hand, *H. sapiens* significantly increased its niche tolerance through time (48 ka: difference = −1.92, $p < 0.001$; 44 ka: difference = −0.14, $p < 0.001$; 40 ka: difference = 2.46, $p < 0.001$), exhibiting the highest increase from the 48 ka time point to the 44 ka time point (difference = −1.69, $p < 0.001$; Figs. 3, S4, S5).

As for niche overlap tests, the first two PCA axes account for > 75% of the total variance in the data (~52% for PC1 and ~24% for PC2). The niches of the two species showed Schoener's D values > 0.6 and reported statistically significant niche similarities ($p < 0.05$) in all the three time frames, with the highest overlap (i.e. Schoener's D = 0.75) at 44 ka.

4. Discussion

Neanderthals were perfectly fit to live in Western Eurasia. They were present there since 150 ka at the very least, and well before the Northern Hemisphere begun experiencing the cold conditions of the last Ice Age. Evidence from mtDNA suggests late Neanderthals were divided into three different populations, occurring in the Middle East, Southern Europe, and Western Europe, respectively (Fabre et al., 2009). Further mtDNA data pointed out to a large genetic diversity in Middle East and Southern European Neanderthals older than 48 ka, while more recent populations inhabiting Western Europe had low mitochondrial genetic variation (Dalen et al., 2012). This is consistent with a scenario of extinction of Northern European populations before 48 ka followed by recolonization from the Middle East, while Southern populations persisted there (Fabre et al., 2009). Therefore, the available evidence seems to confirm the hypothesis of a regional extinction model for North-Western Neanderthal populations in the coldest (Northern) stretches of its habitat (Hublin and Roebroeks, 2009), before the arrival of AMHs. Benito et al. (2017) recently demonstrated *H. neanderthalensis* most suitable environment during the Eemian was the Mediterranean area, while mountain ranges and continental plains showed low habitat suitability. Our data strongly concur on these findings. At 44 and then at 40 ka, (which is in between Heinrich cold events 4 and 5) *H. neanderthalensis* potential range crumbled into a number of little-connected optimal patches, which means its population was steeply reducing in numbers and growing in isolation.

Genetic and demographic data are consistent with these notions. Neanderthals were found to have had small population size and high mortality rates (Bocquet-Appel and Degioanni, 2013; Sørensen, 2011; Trinkaus, 1995). Genetic diversity in late Neanderthals was much lower than in contemporary *H. sapiens* (Krause et al., 2007) and show very low level of heterozygosity (Castellano et al., 2014; Prüfer et al., 2014), and indicate a species split into a number of small and isolated populations (Rogers et al., 2017), which made them prone to inbreeding and outbreeding depression. As a result, Neanderthals might have had at least 40% less fitness than humans on average (Harris and Nielsen, 2016). This is not the same as to say that climatic worsening was the sole factor driving Neanderthals extinct. The close similarity between Neanderthals and (presumed) AMHs climatic preferences makes room for a large effect of competition, in whatever forms it came about. Whether this was competition on the same game species or direct (interference) competition, involving direct killing of Neanderthals by *H. sapiens* individuals (as expected by intraguild competition between carnivore species, Palomares and Caro, 1999), it remains to be elucidated. Hortolà and Martínez-Navarro (2013) propended for this latter, perhaps extreme view. Banks et al. (2008) found that the retraction of Neanderthals to the South during Greenland Inderstadial 8 (almost in coincidence to the moment of extinction) was not due to climatic effect, but to a form of active displacement by modern humans (Banks et al., 2008). References to such displacement are very common in the scientific literature. Villa and Roebroeks (2014) recently referred to this view as a “superiority complex” with little archaeological evidence. In addition, in *H. sapiens* fossil sites, arctic, furred animals are disproportionately represented, while, in comparison to modern humans, remains of *H. neanderthalensis* seem to be associated to warm adapted species (Stewart, 2004) indicating the scope for direct competition over common resources may have been probably narrow (Banks et al., 2008).

According to the model of Gilpin et al. (2016) either cultural differences or rapid population growth in AMHs (both of them being true) may have given the scant and isolated populations of *H. neanderthalensis* a final blow. The molar microwear texture analysis of Neanderthals and modern humans during the last stages of the former existence indicates

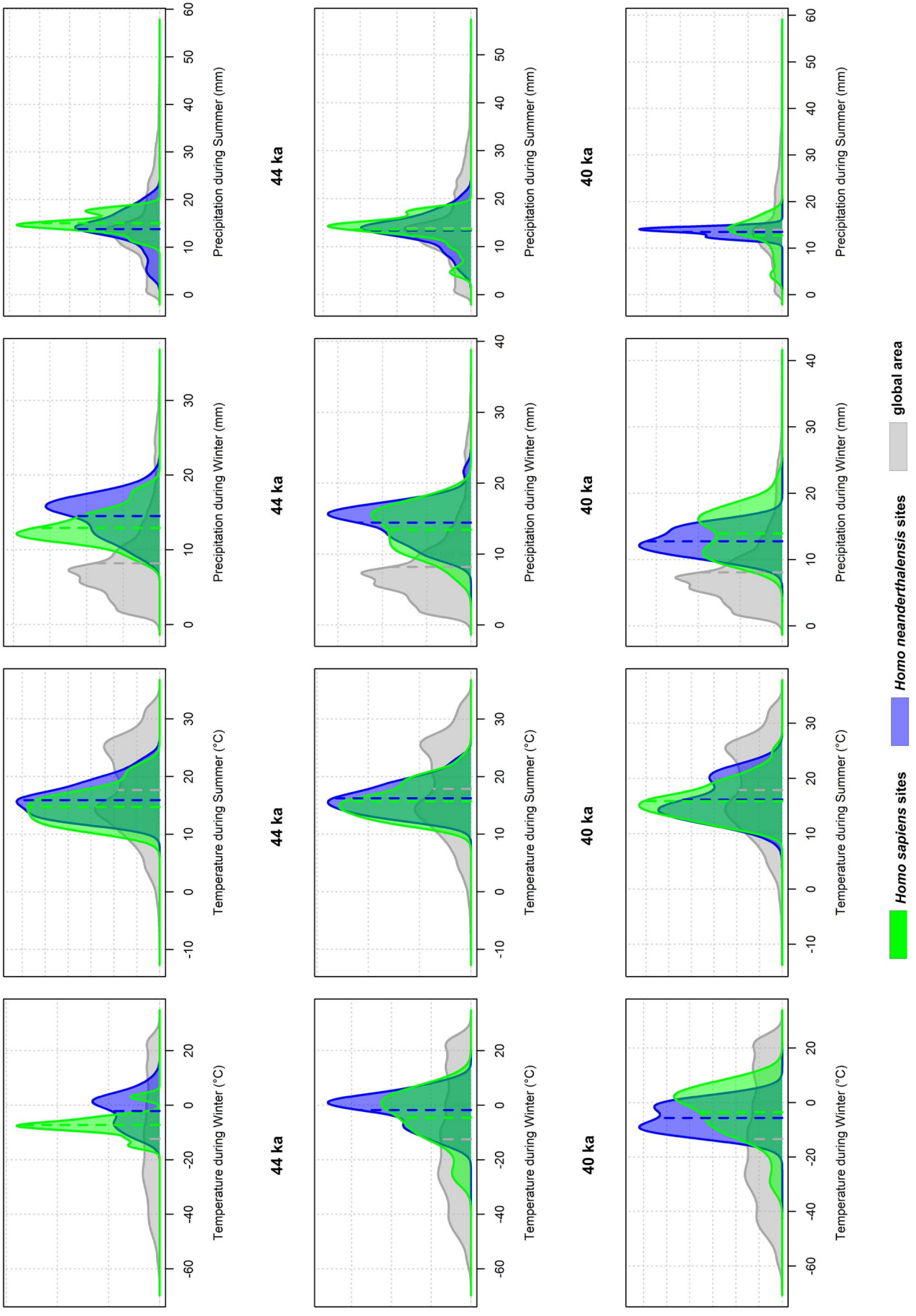

Fig. 3. Kernel densities of climatic predictors values at *H. neanderthalensis* (blue) and *H. sapiens* (green) occurrence sites and in the global area (grey). Dashed lines indicate the mean of each distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that Neanderthals had to change their dietary habits in the face of climate change (El Zaatari et al., 2016), and went through hard times when climate turned extremely cold (Hodgkins et al., 2016). In contrast, *H. sapiens* reacted by expanding its ecological niche (Banks et al., 2013). Together with lower fertility and higher mortality in Neanderthals, and in keeping with our results, this indicate that *H. sapiens* fared better than *H. neanderthalensis* when global climates swung towards the very cold conditions of the latest Pleistocene.

Despite the consistent evidence we found, we urge the reader to consider our results with caution. The presence of AMHs in Europe could have been limited to the very latest Neanderthals (Benazzi et al., 2011), reducing the scope for direct competition. A number of sites/fossil layers may have uncertain attribution (e.g. Geissenklosterle, El Castillo, Grotta del Cavallo), and dated material and specific cultural layers are not always unambiguously associated. We preferred not to modify the original records as they are reported in the databases we refer to, in order to avoid influencing the dataset composition with our own opinions, and projected the potential niche of *H. sapiens* beyond (i.e. before) its actual presence in Europe. Thus, our insights on niche comparisons between the two species are only valid if SDM correctly projects the AMHs niche back in time, and if erroneous attribution to either species are minor in the original data. We are positive about the first point, while it is hard to judge the second, because this means assuming that the niche of AMHs remained stable. However, it is worth noticing here we approximated the fundamental niche of AMHs by pooling all point occurrences together for SDM calibration, that would reduce the impact of possible niche change anyway. Still, we argue it is unsafe interpreting the results at various time steps as they are. Rather than trusting them at face value, we argue what our study really suggests is that Neanderthals niche deteriorated through time. This is almost independent of data quality and the reliability of AMHs climatic niche projection back in time. Beyond dating uncertainty, niche characteristics for *H. sapiens* did not change significantly over time, perhaps suggesting they were better equipped to face with climatic cooling (Banks et al., 2013). We deem a formal analysis of population viability in Neanderthals is required to ascertain whether competition effects are required to explain the disappearance of *H. neanderthalensis* at 40 ka.

5. Conclusions

In this study we modeled potential niche structure and evolution for *Homo neanderthalensis* and *Homo sapiens*, while accounting for fossil layers dating uncertainty. We found that the potential niche of Neanderthals reduced significantly both in size and spatial continuity since 48 ka. While the size of the potential geographic range for *H. sapiens* reduced significantly as well, optimal habitat patches remained much more well connected than in Neanderthals. While the modelling approach we followed and the scarce presence of *H. sapiens* in Europe before 40 ka do not allow to address the issue of the role modern humans played in Neanderthals extinction, our data suggest the changing climatic conditions jeopardized their survival, in keeping with paleogenetic data suggesting *H. neanderthalensis* population was split in little-connected, small demes just prior to extinction.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.01.031.

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Author contributions

M.M. and P.R. conceived the starting idea. M.M, A.M., S.C., C.S, G.T., M.P., and V.V. collected the data. M.D.F. and F.C. performed the analyses. All the authors contributed equally to develop the ideas, analyses and writing of the manuscript.

Additional information

The authors declare no competing financial interests.

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